

## MORPHOLOGICAL AND BEHAVIORAL DEFENSES OF TROCHOPHORE LARVAE OF *SABELLARIA CEMENTARIUM* (POLYCHAETA) AGAINST FOUR PLANKTONIC PREDATORS

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### ABSTRACT

Controlled experiments were conducted by offering eggs, pre-setal trochophores, and setose trochophores of the polychaete *Sabellaria cementarium* to four planktonic predators, *Pleurobrachia bachei* (Ctenophora), *Aequorea victoria* (Hydrozoa), brachyuran megalopa (Crustacea), and juvenile *Sebastes* spp. (Pisces). Each predator species captures prey with different mechanisms and the prey, while similar in size, differ in motility and presence or absence of setae.

Consumption of non-motile eggs was greater by megalopa but less by *A. victoria* than consumption of pre-setal trochophores; it is suggested that differences in predator feeding mechanisms account for these differences. Setose trochophores were always consumed at lower rates than the younger stages. The evidence suggests that setae can function in larval defense against an array of predators with different feeding mechanisms, but that swimming may increase, decrease, or have no effect upon rate of predation, depending upon predator species.

### INTRODUCTION

Thorson (1946), Young and Chia (in press), and others have suggested that the major source of larval mortality for benthic marine invertebrates is predation. While this conjecture may be true, little empirical information supports it. Predation upon invertebrate larvae is generally documented during gut content analyses of predators; larvae usually constitute a minor portion of the diet (reviewed by Young and Chia, in press), and larvae thus observed are often partially digested and therefore difficult to identify. However, Cowden *et al.* (1984) provide data on differential predation upon several pelagic larvae by two benthic filter-feeders. Models of reproductive strategies of benthic invertebrates have generally assumed that rates of predation upon larvae are constant throughout ontogeny (Vance, 1973; Pechenik, 1979; Jackson and Strathmann, 1981), though Christiansen and Fenchel (1979) did consider large, late-stage larvae less susceptible to predation than small, early larvae.

Motility is a factor which may alter rates of predation upon developing larvae. Gerritsen and Strickler (1977) have predicted on the basis of encounter rates that prey could minimize predation by minimizing movement. However, it remains unclear whether diversity of planktivores and feeding mechanisms will render this hypothesis relatively unimportant in marine environments, especially for slow-swimming invertebrate larvae.

A second factor which may alter rates of larval predation is the development of structures such as larval setae (Fig. 1d). A wide variety of planktonic organisms develop setae or spines, including larvae of many benthic polychaetes (Bhaud and

Cazaux, 1982; review by Schroeder and Hermans, 1975) and articulate brachiopods (Long, 1964). These larval setae project posteriorly during normal swimming, but are erected to spread out radially when larvae encounter objects or are otherwise disturbed (Fig. 1b-c). Since larval setae are typically lost during metamorphosis, they are presumed to be adaptations to pelagic existence. Setae and spines have been postulated to function both as "parachutes" which slow sinking rates and as defense mechanisms (Wilson, 1929, 1932; Hardy, 1956; Blake, 1969; Fauchald, 1974; Schroeder and Hermans, 1975). In defense, setae are presumed to function both by increasing a larva's effective size and by making it difficult to swallow. Spines of freshwater rotifers and cladocerans are known to be effective defenses against small plantivorous invertebrates, but are apparently not effective against fish predation (Gilbert, 1966; Dodson, 1974; Kerfoot, 1975, 1978, 1980). The only observations regarding the function of setae or spines for marine organisms are those of Lebour (1919) and Wilson (1929). Lebour (1919) observed a megalopa's dorsal spine lodging the larva into the esophagus of a small fish; the fish was neither able to expel or ingest it and eventually died. Wilson (1929) described small fish ejecting *Sabellaria alveolata* trochophores from their mouths and suggested that erected setae rendered the trochophores offensive.

This study was designed to examine whether motility and setae of trochophores of the polychaete *Sabellaria cementarium* Moore are effective defenses against predation by four planktonic predators. *S. cementarium* was used as prey because its embryos and larvae were readily available, and because of the prominent setae that its trochophores develop (Fig. 1b-d).

#### MATERIALS AND METHODS

Adult *Sabellaria cementarium* were dredged in the vicinity of San Juan Island, Washington. Gametes were obtained and embryos and larvae were cultured as in Smith (1981). Non-motile eggs, 2 day-old pre-setal trochophores and 5 day-old setose trochophores were used as prey (Fig. 1a-c). Body size and shape was relatively constant during the first five days of development (70-90  $\mu\text{m}$ ), though eggs were disk-shaped and somewhat broader when freshly spawned.

Predator species from four phyla, *Pleurobrachia bachei* (Ctenophora), a medusa *Aequorea victoria* (Hydrozoa), unidentified brachyuran megalopa (Crustacea), and juvenile *Sebastes* sp. (Pisces), were chosen because they were common near Friday Harbor during summertime, and because of their different feeding mechanisms. Although in some cases predators were kept in the laboratory for several days before experiments and fed *Artemia salina* nauplii or goldfish food, they appeared to be in good condition at the time of experiments.

For each experiment fifty eggs or larvae were placed into each of 16 1.0 l jars which contained 960 ml of 3  $\mu\text{m}$  filtered sea water. Twelve of the jars were divided into four sets of three replicates. Each set received a different predator species: (1) one 10 mm diameter *P. bachei* per jar; (2) one 30 mm diameter *A. victoria* per jar; (3) five 3 mm long megalopa per jar; or (4) two 15 mm long *Sebastes* sp. per jar. The four remaining jars served as controls, measuring background mortality and handling errors.

All jars were capped and strapped horizontally around the horizontal axis of a "grazing wheel" which rotated at 1.6 rpm, gently stirring the water and keeping the prey evenly distributed within the jars. Experiments were run for 24 hours in a 12:12 light:dark, 14°C coldroom. At the end of each experiment, predators were removed and water was siphoned from the jars through 41  $\mu\text{m}$  Nitex mesh, concentrating the

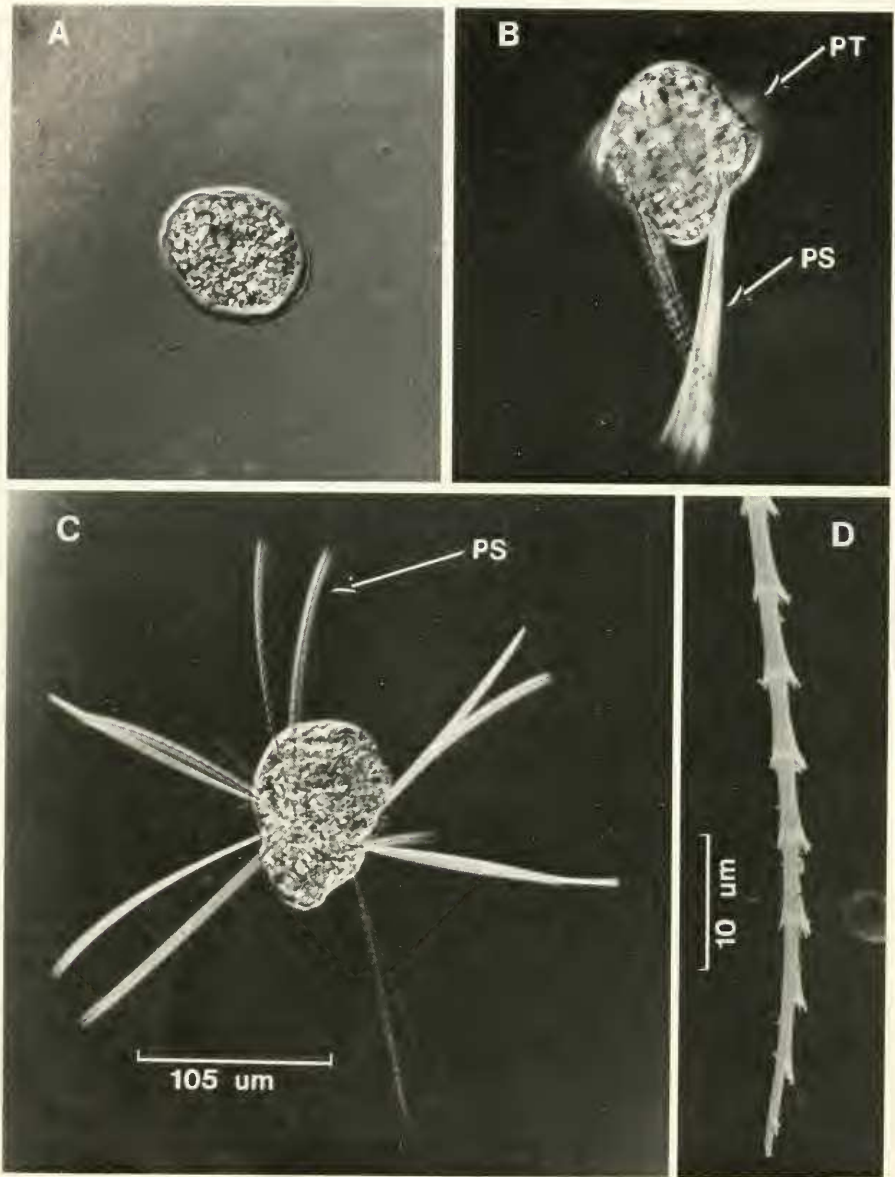


FIGURE 1. Selected developmental stages of *Sabellaria cementarium*; A, B, and C slightly compressed and to same scale. A: unhatched embryo of the same size and shape as eggs and pre-setal trochophores; B: five day-old setose trochophore swimming with unerected setae; C: five day-old trochophore with erected setae; D: seta of *S. cementarium* trochophore. PT, prototroch; PS, provisional setae.

remaining prey in a small volume of residual water. The prey were then washed into vials and preserved in 2% formalin. The preserved prey were later counted in a Bogorov Tray under a dissecting microscope.

Data analysis was performed according to the methods of Zar (1974).

## RESULTS

Predation rate upon the three developmental stages of *Sabellaria cementarium* by each of the four predators is presented in Figures 2a-d. All control values were averaged because loss from control jars was stage-independent; the slope of a least-squares regression of number of larvae missing from controls upon prey stage did not differ significantly from zero (F-test;  $P < .05$ ). A one-way analysis of variance (ANOVA) was calculated from the data for each predator species to determine if there were significant differences between the number of prey missing in the four treatments (controls, eggs, pre-setal trochophores, and setose trochophores). The analyses were done with untransformed data since Bartlett's Test indicated that the data was sufficiently homoskedastic for ANOVA. For all ANOVA's there were significant overall differences between treatments ( $P < .02$  or less), indicating that all predators ate some prey. *A posteriori* Student-Newman-Keuls Range Tests (SNK Tests) were then calculated which compared all possible combinations of treatments and grouped treatment subsets that were not significantly different ( $P < .05$ ).

The different predator species exhibited different rates and patterns of predation upon eggs and pre-setal trochophores, but in all cases setose trochophores were eaten at low rates, not significantly different than control values (Fig. 2). For *Pleurobrachia bachei*, the SNK Test grouped values for the controls and setose trochophores as not different or homogeneous, indicating non-significant predation upon setose trochophores while eggs and pre-setal trochophores were eaten significantly more often.

For *Aequorea victoria* the SNK Test grouped values for the controls, eggs, and setose trochophores as homogeneous, indicating uniformly low rates of loss from

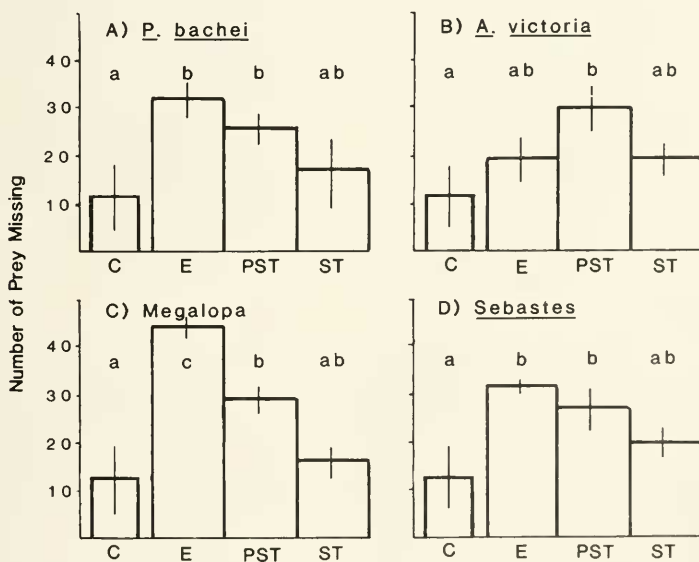


FIGURE 2. Histograms showing mean number of *Sabellaria cementarium* eggs and larvae missing from treatments for each of the four predator species,  $\pm 1$  standard deviation. Treatments are C, controls ( $n = 12$ ); E, eggs ( $n = 3$ ); PST, pre-setal trochophores ( $n = 3$ ); ST, setose trochophores ( $n = 3$ ). Letters over each bar denote the results of a Student-Newman-Keuls Multiple Range Test, where the same letter occurs over two or more bars the bars were grouped as not significantly different ( $P < .05$ ).



these groups. Thus, pre-setal trochophores appear to be vulnerable to predation by *A. victoria*, but eggs and setose trochophores are either neglected or avoided.

The SNK Test indicated that brachyuran megalopa ate significantly more eggs than the other prey stages, but that insignificant numbers of setose trochophores were eaten.

For juvenile *Sebastes* the SNK Test again grouped the controls and setose trochophores as homogeneous, indicating that eggs and pre-setal trochophores combined were eaten significantly more often than setose trochophores.

## DISCUSSION

The effect of motility on predation rate varied among predators, probably a result of the predators' different feeding mechanisms. Predation by medusae involves responses to individual prey in the sense that nematocysts must be stimulated to fire, and prey motion is an important cue in this response (Pantin, 1942). Non-motility may explain the lack of consumption of eggs by *Aequorea victoria*. Prey motion is presumably an important cue for ctenophores and fishes as well, since colloblasts must be stimulated to release adhesive substance in ctenophores (Franc, 1978) and most fish locate prey visually (Kislalioglu and Gibson, 1976; Hyatt, 1979). However, *Pleurobrachia bachei* and *Sebastes* sp. did not eat more motile than nonmotile prey.

Megalopa ate significantly more eggs than all other stages of prey. It thus appears that swimming helped trochophores to escape or avoid these predators. The mechanisms by which most megalopa feed on small prey are not known, but many crustaceans both filter small particles and feed raptorially upon larger prey (Marshall and Orr, 1960; McLaughlin, 1982). If the megalopa did filter-feed, prey capture was probably not dependent upon recognition of individual eggs or trochophores. If so, non-motile eggs would be encountered and captured nearly as often as swimming trochophores, but if swimming enabled some trochophores to escape, the rate of predation upon eggs would be higher, as was observed.

Predation upon setose trochophores was insignificant while oocytes and pre-setal trochophores were eaten more often by all predators (except *A. victoria*, which did not eat eggs). The methods by which setae function defensively have not been investigated, but the radial splay of setae could create at least three potential defenses: (1) the effective size of a larva increases; (2) a buffer zone of setae and water around a larva's tissues is formed; (3) the barbed setae become oriented so that they may pierce objects impinging upon a larva. The possible roles of these mechanisms are discussed below.

Erection of setae increases the overall diameter of a larva, possibly deterring predation by small-mouthed predators as has been shown for freshwater rotifers (Gilbert, 1966). However, the predators used in the present experiments all eat prey much larger than trochophores. Reeve *et al.* (1978) fed *Pseudocalanus minutus* (<650  $\mu\text{m}$  long) to *P. bachei* during production experiments, and Lebour (1924) observed *P. bachei* eating larval fish. *A. victoria* has been commonly observed eating large prey, including fish and other jellyfish (Lebour, 1924; Hyman, 1940; Arai and Jacobs, 1980). The juvenile *Sebastes* sp. fed successfully on *Artemia salina* nauplii (ca. 600  $\mu\text{m}$ ) as well as upon pieces (>1 mm) of goldfish food. Many species of crab larvae are also cultured successfully on *A. salina* nauplii (Rice and Williamson, 1971) and the megalopa used in these experiments fed on goldfish food as well. It thus seems unlikely that the size increase created by setal erection prevents predation by any of the predator species used here. However, megalopa have far smaller mouths than the other predators tested; erected setae may substantially increase handling difficulty if

megalopa cannot swallow larvae whole but must manipulate and dismember them. Similarly, spines of cyclomorphic cladocerans and rotifers have been shown to reduce predation by freshwater predators with small mouths (reviewed by Zaret, 1980). It thus seems probable that setae function defensively against small-mouthed predators such as megalopa by increasing handling time. In contrast, the other predator species used here could easily swallow whole setose *S. cementarium* trochophores.

The buffer zone of sea water surrounding a trochophore with erected setae may be important as a defense against medusae and tentaculate ctenophores. As described above, both *P. bachei* and *A. victoria* must sense and capture individual prey. If a predator's tentacles touch only the erected setae of a trochophore, the tactile or chemical cues necessary to elicit a response may not be perceived. Further, even if a larva is recognized as food, nematocysts and colloblasts may work inefficiently upon setae or across the buffer zone (ca. 150  $\mu\text{m}$ ) of water created by the setae. If trochophores are first trapped by nematocysts or colloblasts, then ingested and finally expelled, their chances of surviving are probably slim. The numerous trochophores surviving experiments appeared to be in good shape; few were deformed or entangled in mucus. It seems unlikely the surviving trochophores were captured at all by these predators, but that setae prevented recognition or prey capture.

Setae may also deter predation by irritating mouthparts as originally implied by Wilson (1929), whose suggestion seems intuitively reasonable because fish capture prey within the buccal cavity where setae could easily pierce oral tissues as trochophores are bitten or swallowed. Predatory fish are also deterred by the spines of sticklebacks (Hoogland *et al.*, 1957), but the spines of some cyclomorphic rotifers and cladocerans are not considered to be effective against fish (Greene, 1983).

Other work on predation upon marine larvae has found patterns of predation comparable to those presented here. For a predator who senses individual prey at a distance, Landry (1978) found that weakly motile early copepod nauplii were poorly detected by the copepod *Labidocera trispinosa*, and were thus eaten at low rates. Large active nauplii were eaten at the highest rates, while copepodids developed an escape response and were eaten rarely. Also, work with marine fish larvae as prey for various crustaceans has generally found that non-motile eggs are not detected by predators and eaten rarely while motile yolk-sac larvae are eaten at high rates. Feeding larvae develop an escape response and are captured and eaten much less often (Lillielund and Lasker, 1971; Theilaker and Lasker, 1974; Bailey and Yen, 1983). The low rates of predation upon later stages in all cases are due to the development of fundamentally new structures or behaviors during ontogeny, processes not observed for freshwater prey (Greene, 1983).

At present it is not possible to assess the potential impact these predators have on pelagic larval populations of *S. cementarium*. No quantitative estimates of the densities of any of the predator or prey species have been made in the Puget Sound area, though all are common in the plankton during summer. Similarly, except for *P. bachei* (see Reeve and Walter, 1978), quantitative observations of the predation rates of the predators upon other prey types have not been made. However, for the predators used we have shown that rates of predation upon setose trochophores are low.

Susceptibility to predation is a ubiquitous and important problem for embryos and larvae of benthic invertebrates (Thorson, 1946; Young and Chia, in press) which should generate strong selective pressures for larval defense. If effective defenses have evolved, larval forms, behaviors, chemicals, and ultimately reproductive strategies should reflect such selection. Reproduction in many benthic invertebrates with pelagic larvae is characterized by a short period of rapid embryogenesis followed by a prolonged

period of larval feeding and growth. This pattern may be facilitated by the development of efficient larval defenses.

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